The Veliger 51(2):66–75 (May 26, 2011)

THE VELIGER

Field Experiments on the Feeding of the Nudibranch *Gymnodoris* spp. (Nudibranchia: Doridina: Gymnodorididae) in Japan

RIE NAKANO AND EUICHI HIROSE

Department of Chemistry, Biology, and Marine Science, Faculty of Science, University of the Ryukyus, Nishihara, Okinawa 903-0213, Japan

Abstract. We report field experiments of the diets of certain *Gymnodoris* species (Nudibranchia: Doridina: Gymnodorididae) that inhabit the seas in the vicinity of Japan. Of 21 individuals of five predatory species, 13 fed on 14 of the 44 prey individuals. Among these predators, five individuals of four species located the mucus trail of their prey and pursued it. After touching the prey with their oral tentacles, most predators everted the buccal apparatus to capture the prey. Two modes of feeding occurred: biting off part of the prey or swallowing it whole. Some predator and prey combinations have not previously been reported, to our knowledge: *Gymnodoris alba* fed on *Vayssierea felis* (Nudibranchia: Doridina: Vayssiereidae), and *G. okinawae* fed on *Metaruncina setoensis* (Cephalaspidea: Runcinidae). We also found an unknown gymnodorid that fed on several *Elysia* spp. and *Thuridilla vatae*. The unknown predator was similar in morphology to *G. alba*, but its prey items were similar to those of *G. okinawae*.

INTRODUCTION

The opisthobranchs (Gastropoda: Mollusca) demonstrate various food habits: Sacoglossa, Anaspidea, and some species of Cephalaspidea are herbivorous, and others are carnivorous (see Behrens, 2005). Carnivorous opisthobranchs feed on specific prey items, including sponges, hydroids, bryozoans, entoprocts, and ascidians; for example, each sponge-feeding species feeds only on specific sponge species (Rudman & Bergquist, 2007).

Many carnivorous species feed on opisthobranchs, as well as on nonopisthobranchs. For example, Cattaneo-Vietti et al. (1993) reported that *Pleurobranchaea maculata* (Quoy & Gaimard, 1832) (Notaspidea: Pleurobranchidae) fed on polychaete worms, amphipods, ophiuroids, dead squids, and dead fishes, as well as opisthobranchs, e.g., *Philine argentata* Gould, 1859 (Cephalaspidea: Philinidae), *Ringicula doliaris* Gould, 1860 (Cephalaspidea: Ringiculidae), and their conspecifics. Among the opisthobranchs that are known to feed on other opisthobranchs are *Chelidonura* spp., *Navanax inermis* (Cooper, 1863), *Philinopsis* spp., *Pleurobranchaea maculata* (Quoy & Gaimard, 1832), *Gymnodoris* spp., *Roboastra leonis* Pola, Cervera & Gosliner 2005, *Melibe* spp., and *Godiva* sp. (Paine, 1963; Kay & Young, 1969; Rudman, 1972; Farmer, 1978; Kay, 1979; Gosliner, 1987; Cattaneo-Vietti et al., 1993; Gosliner et al., 1996; Battle & Nybakken, 1998).

Gymnodorids (Nudibranchia: Doridina: Gymnodorididae) usually feed on opisthobranchs and/or their eggs, but not on other organisms. *Gymnodoris nigricolor* Baba, 1960 is one exception that apparently captures certain goby species (Osumi & Yamasu, 1994), such as *Amblyeleotris japonica* (Williams & Williams, 1986), by grasping their fins with the buccal apparatus. This species does not eat the entire goby, but just the fleshy tissues of the fins. The diet of each gymnodorid encompasses a particular range of species, with some feeding on various orders of nudibranchs and some having more selective diets. For instance, *G. rubropapulosa* (Bergh, 1905) feeds on various genera of the family Chromodorididae, including *Hypselodoris iacula* Gosliner & Johnson, 1999, *H. festiva* Adams, 1861, *Chromodoris annae* Bergh, 1877, *C. strigata* Rudman, 1982, *Chromodoris* sp., and *Mexichromis multituberculata* (Baba, 1953) (Behrens, 2005; Nakano et al., 2007), whereas *G. aurita* (Gould, 1852) is known to feed only on *Marionia* spp. (Nudibranchia: Dendronotina: Tritoniidae) (Behrens, 2005).

The diet species of 11 gymnodorids have been reported. Table 1 summarizes the predator/prey species, including some unpublished observations (Takasaki, Natani, Hoson, Matsuda, personal communications: see Figure 1). The diets of some gymnodorids in Table 1 are laboratory diets (Young, 1969; Hughes, 1983; Johnson & Boucher, 1983) and may not represent natural food habits. The laboratory conditions may also have resulted in unusual opisthobranch behaviors. For example, Johnson & Boucher (1983) reported that *G. okinawae* Baba, 1936 did not feed on *Elysia* in aquaria, but Nakano et al. (2007) observed *G. okinawae* feeding on *Elysia* spp. in the field.

Field observations are more reliable than laboratory observations in understanding natural food habits;

Table 1

Summary of the preceding studies on the diets of *Gymnodoris* spp.

Predator	Prey	Condition	Reference
G. alba (Bergh, 1877)	*Aeolidiella* sp.	Undescribed	Kay & Young, 1969; Kay, 1979
	Favorinus sp.	Undescribed	Kay & Young, 1969; Kay, 1979
	Sakuraeolis modesta	Laboratory	Hughes, 1983
	Flabellina alisonae	Laboratory	Hughes, 1983
	Phyllodesmium sp.	Laboratory	Hughes, 1983
	Aeolidina sp.*	Field	Takasaki (personal communication)
	Phidiana indica	Field	Natani (personal communication)
	Cratena lineata	Field	Matsuda & Hoson (personal communication)
G. amakusana (Baba, 1996)†	*Elysia ornata*	Field	Nakano et al., 2007
G. aurita (Gould, 1852)	*Marionia* sp.	Field	Behrens, 2005
G. bicolor (Alder & Hancock, 1866; <*G. citrina*?)‡	Members of *Gymnodoris*	Undescribed	Young, 1969
	Gymnodoris okinawae	Undescribed	Young, 1969; Kay & Young, 1969; Kay, 1979
	The egg masses of *Gymnodoris okinawae*	Undescribed	Young, 1969
	Gymnodoris plebeia	Undescribed	Young, 1969; Kay & Young, 1969; Kay, 1979
G. ceylonica (Kelaart, 1858)	*Stylocheilus longicauda*	Undescribed	Johnson & Boucher, 1983; Rudman, 1999a, b
	Nakamigawaia sp.§	Field	Nakano et al., 2007
G. citrina (Bergh, 1875)	*Gymnodoris citrina*	Laboratory	Young, 1969
	Gymnodoris citrina	Field	Johnson & Boucher, 1983; Johnson, 1992
	Gymnodoris okinawae	Field	Johnson, 1992; Nakano et al., 2007
	Gymnodoris plebeia	Field	Johnson, 1992
	Several *Gymnodoris* species	Field	Johnson & Boucher, 1983
	Unknown *Gymnodoris* spp.	Field	Johnson, 1992
	Eggs of other *Gymnodoris* species	Field	Johnson & Boucher, 1983; Johnson, 1992
	Eggs of *Gymnodoris ceylonica*	Field	Johnson, 1992
	Eggs of nudibranch	Field	Nakano et al., 2007
G. inornata Bergh, 1880	*Chromodoris orientalis*	Laboratory	Hughes, 1983
	Doriopsilla miniata	Laboratory	Hughes, 1983
	Gymnodoris rubropapulosa	Field	Nakano et al., 2007
	Dendrodoris fumata	Field	Nakano et al., 2007
	Glossodoris rufomarginata‖	Field	Natani (personal communication)
G. okinawae Baba, 1936	Various species of the genus *Elysia*	Undescribed	Kay & Young, 1969
	Members of Elysiidae	Undescribed	Young, 1969
	Cephalaspidean	Undescribed	Johnson & Boucher, 1983
	Did not eat *Elysia*	Laboratory	Johnson & Boucher, 1983
	Thuridilla sp.¶	Field	Nakano et al., 2007
G. rubropapulosa (Bergh, 1905)	*Hypselodoris iacula*	Field	Behrens, 2005
	Chromodoris annae	Field	Nakano et al., 2007
	Chromodoris strigata	Field	Nakano et al., 2007
	Chromodoris sp.#	Field	Nakano et al., 2007
	Hypselodoris festiva	Field	Nakano et al., 2007
	Mexichromis multituberculata	Field	Nakano et al., 2007
G. striata (Eliot, 1908)	*Plakobranchus ocellatus*	Field and laboratory	Johnson & Boucher, 1983
Gymnodoris sp. A**	*Glossodoris cincta*	Field	Nakano et al., 2007

* Conspecific with Nakano (2004) No. 658.

† Rudman (1999c) referred *G. amakusana* as a junior synonym of *G. striata*.

‡ *Gymnodoris bicolor* (Alder & Hancock, 1866) is regarded as a junior synonym of *G. citrina* (Bergh, 1875) by many authors (e.g., Risbec, 1953; MacNae, 1958; Baba, 1960; Young, 1967), although Young (1969) described their internal morphologies discriminate *G. bicolor* from *G. citrina*.

§ "Kurobouzu" is the Japanese common name.

‖ *Gymnodoris inornata* bit off the mantle of *Glossodoris rufomarginata*.

¶ "Fujiiro-midorigai" is the Japanese common name.

"Kongasuri-umiushi" is the Japanese common name.

** "Shirobonbon-umiushi" is the Japanese common name.

Figure 1. *Gymnodoris* species feeding on opisthobranchs in their natural habitats. **A,** *G. alba* (left) feeding on an unknown species of suborder Aeolidina (right); **B,** *G. alba* (right) feeding on *Cratena lineata* (left); **C,** *G. alba* (left) feeding on *Phidiana indica* (right); **D,** *G. inornata* (left) feeding on *Glossodoris rufomarginata* (right). These photographs were provided by Kenji Takasaki (**A**), Tomohiro Natani (**B** and **D**), and Sayoko Matsuda (**C**). Scale bars = 10 mm.

Figure 2. *Gymnodoris okinawae* feeding on prey (p), *Elysia* sp. B. **A,** The predator bit the posterior part of the parapodia of the prey; **B,** The prey escaped by cutting off the parapodia (arrow), which the predator ate. Scale bar = 5 mm.

however, the field offers only chance encounters with feeding opisthobranchs, and accumulating numerous observations is difficult. Thus, an experimental approach in the field is necessary to demonstrate the range of prey species of *Gymnodoris* spp. Our field experiments were designed to reveal the range and specificity of gymnodorid diets *in situ*: we offered several opisthobranch species to gymnodorids in the field and observed whether the predators fed on the prey candidates. We also recorded the distance at which each predator first noticed the prey.

MATERIALS AND METHODS

Animals

From 2006 to 2008, we scuba- and skin-dove to collect gymnodorids and prey candidates to examine the diets of some *Gymnodoris* species inhabiting subtropical and warm temperate waters in the vicinity of Japan. Table 2 lists the collection sites, dates, and habitats. Upon collection, we measured the body length, collection depth, and water temperature of each individual. The specimens were temporarily kept in a

Table 2

Gymnodoris spp., and their prey: field experiment.

Predator	Collection site*	Body length (mm)	Prey	Collection site	Body length (mm)	Depth (m)	Water temperature (°C)	Habitat	Distance† (mm)	Feeding behavior‡	Date
G. alba No. 1	A	10	*Vayssierea felis*	A	2	Intertidal	16	Rock	10	Swallowed up	April 19, 2006
			Egg of *Vayssierea felis*	A	1.5	Intertidal	16	Rock	10	Swallowed up	April 19, 2006
G. citrina No. 1	A	15	*Vayssierea felis*	A	2	Intertidal	16	Rock	—	Ignored	April 19, 2006
			Egg of *Vayssierea felis*	A	1.5	Intertidal	16	Rock	—	Ignored	April 19, 2006
			Gymnodoris alba	F	10	Intertidal	16	Rock	0	Swallowed up	April 19, 2006
G. citrina No. 2	F	20	*Thuridilla carlsoni*	F	20	11	29	Dead coral	—	Ignored	August 26, 2006
			Chromodoris rufomaculata	F	5	11	29	Dead coral	—	Ignored	August 26, 2006
			Glossodoris rufomarginata	F	20	7	29	Dead coral	—	Ignored	August 26, 2006
			Roboastra gracilis	F	10	7	29	Dead coral	—	Ignored	August 26, 2006
			Chelidonura inornata	E	10	8	29	Sand	—	Ignored	August 27, 2006
			Elysia sp. A	E	4	18	29	Dead coral	—	Ignored	August 27, 2006
			Halgerda tessellata	E	10	18	29	Dead coral	—	Ignored	August 27, 2006
			Nembrotha milleri	E	80	16	29	Dead coral	—	Ignored	August 27, 2006
			Chromodoris fidelis	E	10	8.5	29	Dead coral	—	Ignored	August 27, 2006
			Baeolidia japonica	E	5	6	29	Dead coral	—	Ignored	August 27, 2006
			Gymnodoris citrina	E	8	4.5	29	Dead coral	0	Swallowed up	August 27, 2006
			Sagaminopteron psychedelicum	E	5	4.5	29	Dead coral	—	Ignored	August 27, 2006
G. citrina No. 3	E	12	*Gymnodoris okinawae*	E	12	6.2	25	Dead coral	0	Swallowed up	August 28, 2006
			Hexabranchus sanguineus	E	4	6.5	25	Dead coral	10	Touched with oral tentacles	August 28, 2006
G. citrina No. 4	B	10	*Gastropteron* sp.§	B	3	5	20	Rock, occasional coral	—	Ignored	January 21, 2007
G. citrina No. 5	B	20	*Chelidonura amoena*	B	20	7	20	Rock, occasional coral	—	Ignored	January 21, 2007
G. citrina No. 6	E	10	*Thuridilla carlsoni*	E	25	5.6	25	Dead coral	—	Ignored	May 24, 2007
			Dendrodoris denisoni	E	55	5.	25	Dead coral	—	Ignored	May 24, 2007
			Chromodoris aureopurpurea	E	20	4	25	Dead coral	—	Ignored	May 24, 2007
G. citrina No. 7	B	12	*Gymnodoris okinawae*	B	8	2	23	Rock, occasional coral	80	Swallowed up	November 15, 2007
G. okinawae No. 1	E	12	*Gymnodoris okinawae*	E	10	4.5	25	Dead coral	—	Ignored	August 27, 2006
			Thuridilla vatae	E	10	6.2	25	Dead coral	—	Ignored	August 28, 2006
G. okinawae No. 2	E	10	*Elysia mercieri*	E	4	6.8	25	Dead coral	30	Swallowed up	August 28, 2006
G. okinawae No. 3	B	5	*Elysia lobata*	B	5	5	20	Rock, occasional coral	0	Bit off and partly fed‖	January 22, 2007

Table 2

Continued.

Predator	Collection site*	Body length (mm)	Prey	Collection site	Body length (mm)	Depth (m)	Water temperature (°C)	Habitat	Distance† (mm)	Feeding behavior‡	Date
G. okinawae No. 4	B	NR	*Metaruncina setoensis*	B	1	2	20	Rock, occasional coral	0	Swallowed up	January 22, 2007
G. okinawae No. 5	C	8	*Elysia* sp. B¶	C	5	7	24	Mud	10	Swallowed up	May 11, 2007
G. okinawae No. 6	B	10	*Thuridilla carlsoni*	B	10	4	22	Rock, occasional coral	—	Ignored	November 13, 2007
G. okinawae No. 7	E	15	*Cyerce* sp.#	E	4	4	25	Dead coral	—	Ignored	May 24, 2007
			Noumea simplex	E	7	6	25	Dead coral	—	Ignored	May 24, 2007
			Favorinus japonicus	E	15	4	25	Dead coral	—	Ignored	May 24, 2007
			Egg mass of nudibranch	E	—	4	25	Dead coral	—	Ignored	May 24, 2007
			Moridilla brockii	E	20	5	25	Dead coral	—	Ignored	May 24, 2007
G. rubropapulosa No. 1	C	80	*Chromodoris aureopurpurea*	C	30	8	22	Mud	0	Bit off and partly fed	May 3, 2007
G. rubropapulosa No. 2	C	70	*Chromodoris coi*	C	30	8	22	Mud	0	Bit off and partly fed	May 3, 2007
Gymnodoris sp. B No.	E	15	*Thuridilla vatae*	E	5	6	23	Dead coral	10	Swallowed up	January 13, 2008
Gymnodoris sp. B No. 2	D	15	*Chromodoris verrieri*	D	3	1	22	Rock, seagrass	—	Ignored	April 3, 2008
Gymnodoris sp. B No. 3	D	13	*Elysia ornata*	D	8	Intertidal	22	Rock, seagrass	0	Swallowed up	April 20, 2008
Gymnodoris sp. B No. 4	D	10	*Thuridilla kathae*	D	20	Intertidal	23	Rock, seagrass	0	Everted the buccal apparatus	April 25, 2008
			Thuridilla albopustulosa	D	3	Intertidal	23	Rock, seagrass	0	Touched with oral tentacles	April 25, 2008
			Thuridilla splendens	D	4	Intertidal	23	Rock, seagrass	—	Ignored	April 25, 2008
			Thuridilla gracilis	D	15	Intertidal	23	Rock, seagrass	—	Ignored	April 25, 2008

* A, Manazuru Kanagawa (35°8′N, 139°9′E); B, Hachijo Island, Tokyo (33°6′N, 139°46′E); C, Kin Okinawa Island, Okinawa (26°26′N, 127°56′E); D, Tengan Okinawa Island, Okinawa (26°24′N, 127°50′E); E, Zamami Island, Okinawa (26°13′N, 127°17′E); F, Gahi Island, Okinawa (26°12′N, 127°17′E).

† The distance at which the predator initiated the feeding behavior. "—" indicates no response at 0 mm.

‡ Processes of feeding behavior of each *Gymnodoris* individual.

§ Conspecific with Nakano (2004) No. 41.

|| Predator fed on prey's parapodia only. Other parts of prey—head and foot, including pericardium—ran away from predator.

¶ Conspecific with Ono (2004) No. 101. "Tsunokuro-midorigai" is the Japanese common name.

Conspecific with Ono (2004) No. 130. "Kihoshiuroko-umiushi" is the Japanese common name.

NR=No Record.

collecting jar until the *in situ* feeding experiment, which occurred when we found prey candidates (i.e., other opisthobranchs or their eggs).

We found an unknown gymnodorid that has been recorded from the intertidal zone to about 10 m deep in the vicinity of the Okinawa Islands. The morphology of this species is similar to that of *G. alba* (Bergh, 1877) in having the genital orifice immediately posterior to the cephalic hood. However, this unknown *Gymnodoris* species is distinguished from *G. alba* by its body colors: the dorsum of this species is a translucent brown covered with small yellow spots, whereas *G. alba* has an opaque white body covered with small red spots. Moreover, this *Gymnodoris* species has a square white patch in front of the gill and a triangular white patch between the rhinophores, whereas *G. alba* never has white patches. Therefore, we regarded this species as a undescribed species, i.e., *Gymnodoris* sp. B in this report.

Feeding Experiment

The gymnodorid predator was placed 80 mm from the prey candidate (another opisthobranch), on its mucus trail, and the behavior of the predator was then recorded with a video or digital camera encased in a waterproof housing. If the predator caught the prey candidate, the mode of feeding was recorded as swallowing the prey whole, sucking its body fluid, or biting off part of its body. If the predator did not chase the prey candidate within 3 min, the mucus trail distance to the prey was shortened to 30 mm. If the predator did not follow the candidate within another 3 min, the mucus trail distance was shortened to 10 mm. Then, if the predator did not pursue the prey within 3 min, it was placed on the prey candidate. If the predator did not show any feeding behavior within 3 min, we concluded that the candidate was not a prey species of the gymnodorid.

We conducted the same experiment with nudibranch egg masses: initially, the predator was placed 80 mm from the egg mass, with the distance shortened every 3 min, to 30 mm, to 10 mm, and to 0 mm, if the predator did not move toward the eggs.

RESULTS

Prey Species of *Gymnodoris* spp.

In our feeding experiments, 21 individuals of five *Gymnodoris* species were examined against 46 individuals of 38 prey candidate species. Of the gymnodorids, 13 individuals (five species) fed on 14 prey individuals (13 species). Table 2 summarizes the results. To our knowledge, we are newly reporting two combinations of predator–prey species: *G. alba* (Bergh, 1877) No. 1 feeding on *Vayssierea felis* (Collingwood, 1881) (Nudibranchia: Doridina: Vayssiereidae) and *G. okinawae* No. 4 feeding on *Metaruncina setoensis* (Baba, 1954) (Cephalaspidea: Runcinidae).

Feeding Behavior Processes and Distance to Locate Prey

Gymnodorids engaged in the following feeding behaviors: first, the gymnodorid predator located the mucus trail of the prey and pursued the prey. Upon reaching the prey, the predator touched the prey with its oral tentacles, and then usually everted the buccal apparatus to capture the prey. A few predators did not do this and ignored the prey. After everting the buccal apparatus, some predators fed on the prey, but others did not. Those that fed used one of the three modes detailed in the next section. Nonfeeders retracted the buccal apparatus and freed the prey candidate. Some predators did not notice or did not follow the mucus trail of the prey candidate. Even when we set the gymnodorid directly on a prey candidate, some predators ignored it.

Among the 14 gymnodorid individuals that fed on prey, five predators (four species) located and pursued the prey before touching it. *Gymnodoris citrina* (Bergh, 1875) No. 7 located its prey, *G. okinawae*, from a distance of 80 mm. When the predator almost lost the trail of its prey, it raised its upper body and swung its head from side to side, appearing to search for the prey. After locating the mucus trail again, it followed the trail and swallowed the prey. On the other hand, *G. citrina* No. 3 did not locate *G. okinawae* until we set it directly on the prey. *Gymnodoris citrina* No. 3 fed on the prey immediately after this direct contact. From a distance of 30 mm, *G. okinawae* No. 2 located the mucus trail of *Elysia mercieri* and fed on the prey. From a distance of 10 mm, *G. alba* located and fed on *Vayssierea felis* and its eggs. Similarly, *G. okinawae* No. 5 and *Gymnodoris* sp. B located and fed on *Elysia* sp. B and *Thuridilla vatae* (Risbec, 1928), respectively. Although *G. citrina* No. 3 located *Hexabranchus sanguineus* from a distance of 10 mm and touched it, it did not feed on it.

The other nine predators crawled randomly around the prey mucus trails until they happened to touch the prey, at which point they everted the buccal apparatus to attack, and then fed on the prey. Interestingly, although *G. citrina* No. 1 fed on *G. alba* that had just fed on *Vayssierea felis*, *G. citrina* No. 1 never fed on *V. felis* directly.

Modes of Predation

Three modes of predation have been reported in gymnodorids: biting the prey, swallowing it whole, and sucking the body fluid from the prey (Hughes, 1983; Johnson, 1992; Ono, 1999, 2004; Nakano, 2004; Behrens, 2005; Nakano et al., 2007). We did not observe sucking behavior. After capturing the prey

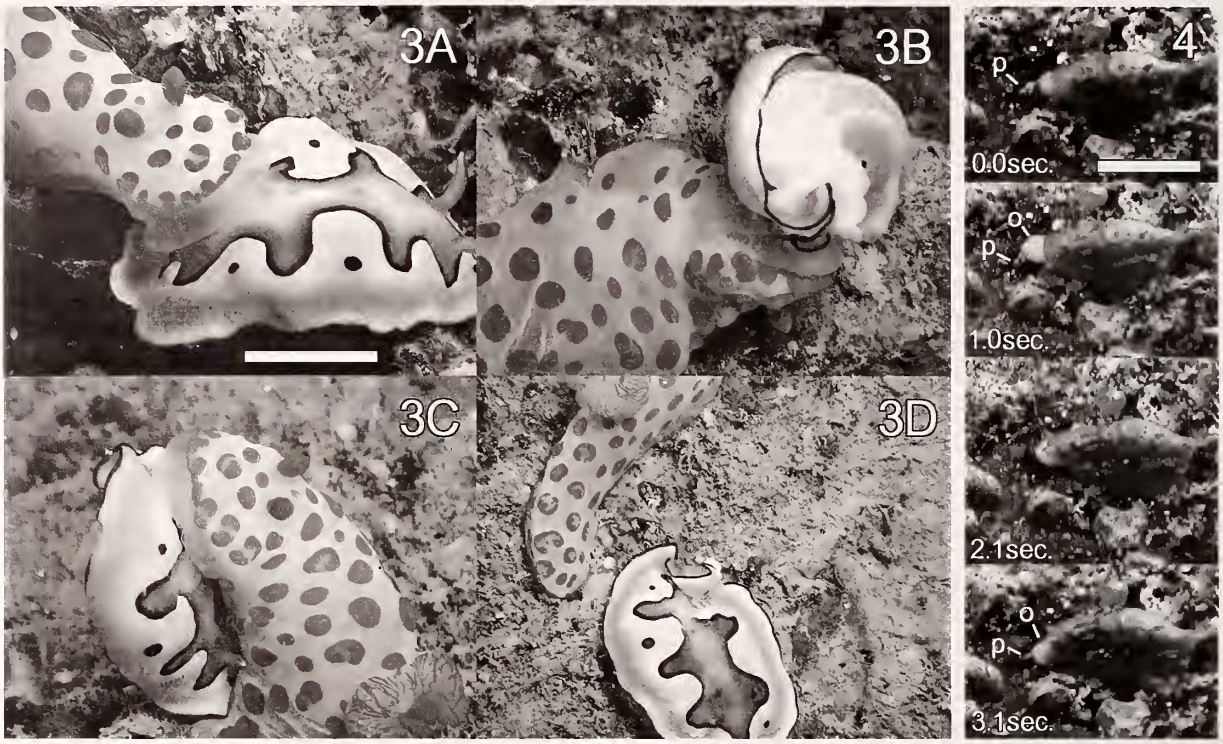

Figure 3. *Gymnodoris rubropapulosa* shook its *Chromodoris coi* prey to bite off the dorsal part. Scale bar = 10 mm.
Figure 4. *Gymnodoris* sp. B grasping a prey (p), *Thuridilla vatae*, with the radula on the odontophore (o). The predator repeatedly extended and retracted the odontophore three times within 9 sec to drag the prey into the esophagus. The images were captured from a video. Scale bar = 10 mm.

with the buccal apparatus, the gymnodorids we observed bit but did not feed on the prey, bit off part of the prey and fed on it partly, or completely devoured the prey.

Gymnodoris okinawae swallowed several *Elysia* species whole, but not *E. lobata* Gould, 1852 and *Elysia* sp. B. When we offered *E. lobata* to *G. okinawae* No. 3, the predator bit off part of the prey, leaving the head. *Elysia* sp. B, known by its Japanese common name "tsunokuro-midorigai" (cf. Ono, 2004), is an undescribed species that is commonly found in southern parts of Japan. When we offered *Elysia* sp. B to *G. okinawae* No. 5, the predator cut off the parapodia of the prey (Figure 2) and swallowed them, but the wounded prey animal, with head and foot, including the pericardium, intact then escaped.

Two *G. rubropapulosa* individuals fed on *Chromodoris aureopurpurea* Collingwood, 1881 and *C. coi* (Risbec, 1956), respectively. In both cases, the predators did not completely swallow their prey. *Gymnodoris rubropapulosa* No. 1 bit *C. aureopurpurea* on its dorsal side and tried to swallow it. About 8 minutes later, *G. rubropapulosa* No. 1 shook the prey, and 13 minutes later, the predator bit off a portion of the prey. The mantle of *C. aureopurpurea* was partly damaged, and the animal had already died. *Gymnodoris rubropapulosa* No. 2 bit *C. coi* on its dorsal side and immediately shook the prey. Fourteen minutes later, the predator bit off part of the prey. Although the mantle of *C. coi* was partly damaged, the prey was still alive (Figure 3).

To feed, *Gymnodoris* sp. B extended its large odontophore from the mouth to grasp the prey with its radula and then retracted the odontophore to drag the prey into its esophagus. The predator repeated the extension and retraction of the odontophore three times within 9 sec, until the prey was dragged into the esophagus (Figure 4).

DISCUSSION

Of the gymnodorids that feed on nudibranchs of various orders, some feed exclusively on particular groups (Kay & Young, 1969; Kay, 1979; Johnson & Boucher, 1983; Hughes, 1983; Johnson, 1992; Behrens, 2005; Nakano et al., 2007). Our *in situ* observations are basically consistent with previous records. However, we note that laboratory experiments may produce abnormal feeding behavior in predators. The unique food habits of gymnodorids will be revealed by the repetition and accumulation of field experiments, using as many species and individuals as possible.

Our study showed that some individuals of *G. alba*, *G. citrina*, *G. okinawae*, and *Gymnodoris* sp. B are occasionally able to locate a mucus trail and pursue their prey before direct contact with the prey, whereas the other individuals of the above four species and all the individuals of *G. rubropapulosa* do not recognize the prey until they touch them (see Table 2). Although gymnodorids are known to swallow their prey whole or suck its body fluids (Young, 1969; Hughes, 1983; Johnson, 1992; Ono, 1999, 2004; Nakano, 2004; Behrens, 2005; Nakano et al., 2007), we found that some predators bit off parts of the prey. In these cases, the predator did not eat the prey completely, and one prey individual escaped without its parapodia. Biting off pieces rather than complete ingestion may be related to body size of prey. It is also possible that the predator chooses to bite off prey when the prey is an unusual prey species for the predator and/or the predator is not hungry. We did not observe sucking behavior in the present study.

Kay & Young (1969), Kay (1979), and Hughes (1983) reported that in the laboratory *G. alba* feeds on several species of the suborder Aeolidina, as did Takasaki, Natani, Hoson, and Matsuda (personal communications), who observed *G. alba* in the field feeding on *Phidiana indica* (Bergh, 1896), *Cratena lineata* (Eliot, 1905), and an undescribed aeolidinan. The undescribed aeolidinan is conspecific to Aeolidina sp. 24 (No. 658) in Nakano (2004). In this study, we observed *G. alba* feeding on *Vayssierea felis* (Nudibranchia: Doridina: Vayssiereidae) and its eggs. *Vayssierea felis* is a small nudibranch (~3 mm long) that inhabits intertidal and subtidal zones of rocky shores in Japan. It is much smaller than the aeolidinans and moves very slowly. Occasionally, we found many *V. felis* in one location. Thus, *V. felis* would be an easily obtainable prey species for *G. alba* that inhabit intertidal and subtidal zones. However, since the habitat of *V. felis* is very restricted, *G. alba* inhabiting deeper sites would not encounter this prey species. As the external features of *G. alba* feeding on *V. felis* and that feeding on an aeolidinan do not differ, we conclude that *G. alba* feed on both *V. felis* and aeolidinans, depending on the habitat.

Gymnodoris okinawae are known to feed on *Elysia* spp. and an undescribed *Thuridilla* sp. (Kay & Young, 1969; Young, 1969; Johnson & Boucher, 1983; Nakano et al., 2007). This undescribed *Thuridilla* species is commonly found in southern Japan and is known by its Japanese common name, "fujiiro-midorigai" (see Ono, 2004). Unfortunately, we could not test "fujiiro-midorigai" as a prey candidate for *G. okinawae* in this study. We observed *G. okinawae* attacking and severing the parapodia of *Elysia* sp. B. This undescribed *Elysia* species is commonly found in southern Japan and is known by its Japanese common name, "tsunokuro-midorigai" (see Ono, 2004). While *G. okinawae* fed on the parapodia, the prey escaped. We still do not know whether this was a type of autotomy on the part of *Elysia* sp. B. Moreover, we observed that *G. okinawae* fed on *Metaruncina setoensis* (Cephalaspidea: Runcinidae), which is a small cephalaspedian (~5 mm long) inhabiting the rocky shores of Japan from the intertidal to the subtidal zones. *Metaruncina setoensis* is much smaller than *Elysia*, moves very slowly, and is often abundant in some locations. As the external morphology of *G. okinawae* feeding on *M. setoensis* does not differ from that feeding on *Elysia* spp. we conclude that *G. okinawae* feeds on both *M. setoensis* and *Elysia* species. Johnson & Boucher (1983) reported that *G. okinawae* fed on a cephalaspidean, which was probably *M. setoensis* or another runcinid closely related to *M. setoensis*.

The feeding behavior of *G. citrina* is unique; this carnivore feeds not only on congeners and their eggs, but also on conspecifics (Johnson, 1992; Nakano et al., 2007). Although we offered 23 opisthobranch individuals (21 species) to seven *G. citrina* individuals as prey candidates, including *Gastropteron* sp. (Cephalaspidea: Gastropteridae), *Elysia* sp. (Sacoglossa), *Vayssierea felis* (Nudibranchia: Doridina), and *Baeolidia japonica* Baba, 1933, (Nudibranchia: Aeolidina), *G. citrina* fed exclusively on gymnodorids (*G. alba*, *G. citrina*, and *G. okinawae*) and was not interested in any of the other prey candidates. Our results were consistent with previous reports (Young, 1969; Johnson & Boucher, 1983; Johnson, 1992; Nakano et al., 2007). *Gymnodoris citrina* No. 3 chased and touched *Hexabranchus sanguineus* (Rüppell & Leuckart, 1828) but did not feed on it. Although it is uncertain why this *G. citrina* pursued the nongymnodorid, some possible explanations include: (1) *H. sanguineus* was not the prey item, and *G. citrina* was following another mucus trail that coincidentally ran along that of *H. sanguineus*; (2) *H. sanguineus* is a prey species, but the predator had just eaten *G. okinawae* and was full; (3) *H. sanguineus* is not a prey species, but its mucus trail contains signals similar to those of *G. citrina* prey.

Nakano et al. (2007) reported from field observations that *G. rubropapulosa* swallowed *Chromodoris strigata*, *Chromodoris* sp., *Hypselodoris festiva*, and *Mexichromis multituberculata* whole. The undescribed *Chromodoris* species is commonly found in the vicinity of Hachijo-jima Island and the Bonin Islands, and is known by its Japanese common name, "kongasuri-umiushi" (see Nakano, 2004). This predator also feeds on *G. rufomarginata* (Bergh, 1890), *Hypselodoris iacula*, *H. dollfusi* (Pruvot-Fol, 1933), *H. krakatoa* Gosliner & Johnson, 1999 and *M. marieri* (Crosse, 1872) (Behrens, 2005; Behrens, personal communication). These observations suggest that *G. rubropapulosa* feeds on chromodoridid family members, usually by swallowing its

prey whole. We observed *G. rubropapulosa* feeding on two other *Chromodoris* species: *C. aureopurpurea* and *C. coi*. However, neither of two *G. rubropapulosa* individuals swallowed their prey, but bit off portions of it within a few minutes. These prey animals (ca. 30 mm) were probably too large for the predators (ca. 80 mm) to swallow. Thus, *G. rubropapulosa* may change its mode of feeding depending on prey size and/or species.

In this study, we discriminate *Gymnodoris* sp. B from *G. alba* based on the difference their body colors. If *Gymnodoris* sp. B were a color morph type of *G. alba*, it should feed on *Vayssierea felis* or species of the suborder Aeolidina. Unfortunately, we were not able to offer it these prey candidates. However, the prey species of *Gymnodoris* sp. B were more similar to those of *G. okinawae* than those of *G. alba*. As described above, *G. okinawae* feeds on *Elysia* spp. but not *Thuridilla* spp. with one exception. In our study, *G. okinawae* ignored *T. vatae*. However, it does feed on *Thuridilla* sp. which is known in Japan as "fujiiro-midorigai." Both *Elysia* and *Thuridilla* belong to the family Elysiidae (Elysioidea). The four *Gymnodoris* sp. B individuals in our study ate *T. vatae* and some *Elysia* species, but not other *Thuridilla* spp., e.g., *T. katae* Gosliner, 1995, *T. splendens* (Baba, 1949), *T. gracilis* (Risbec, 1928) and *T. albopustulosa* Gosliner, 1995. This observation suggests that *Gymnodoris* sp. B differs from *G. okinawae* in its food habits as well as its morphology. Kay & Young (1969) reported that the genital orifice of *G. okinawae* is immediately posterior to the cephalic hood, but we observed it to be halfway between the cephalic hood and the gill. Moreover, the genital orifice of *G. okinawae* is small and inconspicuous. Body colors also discriminate *G. okinawae* from *Gymnodoris* sp. B. Thus, *Gymnodoris* sp. B appears to be an undescribed species, although detailed observations, including internal morphology, are necessary to clarify the taxonomic status of this gymnodorid.

Among the 21 predatory gymnodorid individuals we examined, only *G. citrina* No. 7 located prey at an 80-mm distance. When the predator almost lost the mucus trail of its prey, it raised the upper part of its body and swung its head until it located the mucus trail again. Similar behavior was reported for *Navanax inermis*: "If the trail is chased away from the prey, a characteristic 'searching' behavior is observed at its end. Once contact is lost, *Navanax* swings its head back and forth in small arcs, and eventually may even turn itself around" (Paine, 1963). The *N. inermis* experiment was conducted in a shallow aquarium with a flat sandy bottom, whereas our experiments were conducted in the field at a depth of 2 m. Therefore, the different experimental conditions possibly caused some differences in the feeding behaviors. Alternatively, the two very distantly related opisthobranchs may exhibit different behaviors. Opisthobranchs that feed on opisthobranchs, such as *N. inermis* and *Gymnodoris*, may use chemoreception to locate and chase their prey. The head-swinging behavior of both *N. inermis* and *G. citrina* suggests that these predators perceive diffusible molecules released from the mucus trail and/or the body surface of the prey.

In our study, gymnodorids did not always locate and chase prey effectively. Since both *Gymnodoris* spp. and their prey crawl slowly, we are not sure how they find sufficient prey to survive. Some predators seem to process chemical cues from their prey; however, the cue molecules and reception mechanism(s) of gymnodorids remain to be elucidated.

Acknowledgments. We are indebted to Atsushi Ono (Dive service Ono nyi nyi) and Seiji Takegata for their helpful advice and encouragement. We thank Sayoko Matsuda (Scuba House K's), Yuki Hoson, Kenji Takasaki, and Tomohiro Natani for providing the photographs of *Gymnodoris alba* and *G. inornata* feeding on prey. We also thank Kotaro Tanaka (Diving Club Concolor), Mike C. Miller ("The Slug Site" webmaster), Kaoru Imagawa (Ocean Blue), Hisako Yamada, Haruo Kinoshita, and the members of our laboratory (Yuzo Ota, Aoi Kojima, Kanako Kamegawa, and Nagisa Sugiyama) for their kind help in collecting *Gymnodoris* spp. and prey candidates. This study was partly supported by the 21st Century COE Program of the University of the Ryukyus, Okinawa, Japan.

LITERATURE CITED

BABA, K. 1960. The genera *Gymnodoris* and *Nembrotha* from Japan (Nudibranchia, Polyceridae). Publications of the Seto Marine Biological Laboratory 8:71–74.

BATTLE, K. & J. NYBAKKEN. 1998. The feeding habits of *Pleurobranchaea californica* Macfarland, 1966 (Opisthobranchia: Notaspidea) in Monterey Bay, California. The Veliger 41:213–226.

BEHRENS, D. W. 2005. Nudibranch Behavior. New World Publications: Jacksonville, Florida. 176 pp.

CATTANEO-VIETTI, R., B. BURLANDO & L. SENES. 1993. Life history and diet of *Pleurobranchaea meckelii* (Opisthobranchia: Notaspidea). Journal of Molluscan Studies 59: 309–313.

FARMER, W. M. 1978. *Tambja* and *Roboastra* (Mollusca: Opisthobranchia) from the Gulf of California and the Galapagos Islands. The Veliger 20:375–385.

GOSLINER, T. M. 1987. Nudibranchs of Southern Africa: A Guide to Opisthobranch Molluscs of Southern Africa. Sea Challengers: Monterey, California. vi + 136 pp.

GOSLINER, T. M., D. W. BEHRENS & G. C. WILLIAMS. 1996. Coral Reef Animals of the Indo-Pacific: Animal Life from Africa to Hawaii Exclusive of the Vertebrates. Sea Challengers, Monterey, CA. 320 pp.

HUGHES, H. P. I. 1983. Feeding in *Gymnodoris inornata* (Bergh) and *Gymnodoris alba* (Bergh) (Opisthobranchia). Pp. 627–633 in B. Morton & D. Dudgeon (eds.), Proceedings of the Second International Workshop on the Malacofauna of Hong Kong and southern China, Hong Kong. Hong Kong University Press: Hong Kong.

JOHNSON, S. 1992. Cannibalism and mating in *Gymnodoris citrina* (Bergh, 1877). Hawaiian Shell News 40:3–6.

JOHNSON, S. & L. M. BOUCHER. 1983. Notes on some Opisthobranchia (Mollusca: Gastropoda) from the Marshall Islands, including 57 new records. Pacific Science 37: 251–291.

KAY, E. A. 1979. Hawaiian marine shells, reef and shore fauna of Hawaii, section 4: Mollusca. Bernice P. Bishop Museum Special Publication, 653 pp.

KAY, E. A. & D. K. YOUNG. 1969. The Doridacea (Opisthobranchia, Mollusca) of the Hawaiian Islands. Pacific Science 23:172–131.

MACNAE, W. 1958. The families Polyceridae and Goniodorididae (Mollusca, Nudibranchia) in southern Africa. Transactions of the Royal Society of South Africa 35:341–372.

NAKANO, R. 2004. Opisthobranchs of the Japanese Islands. Rutles: Tokyo. 304 [in Japanese].

NAKANO, R., K. TANAKA, S. DEWA, K. TAKASAKI & A. ONO. 2007. Field observations on the feeding of the Nudibranch *Gymnodoris* spp., in Japan. The Veliger 49:91–96.

ONO, A. 1999. Opisthobranchs of the Kerama Islands. TBS Britannica: Tokyo. 189 pp [in Japanese].

ONO, A. 2004. Opisthobranchs of the Ryukyu Islands. Rutles: Tokyo. 304 pp [in Japanese].

OSUMI, D. & T. YAMASU. 1994. The nudibranch *Gymnodoris nigricolor* Baba, parasitic with marine gobies. Zoological Science 11:54.

PAINE, R. T. 1963. Food recognition and predation on opisthobranchs by *Navanax inermis* (Gastropoda: Opisthobranchia). The Veliger 6:1–9.

RISBEC, J. 1953. Mollusques nudibranches de la Nouvelle-Calédonie. Faune de l'Union Française 15:1–189.

RUDMAN, W. B. 1972. A comparative study of the genus *Philinopsis* Pease, 1860 (Aglajidae, Opisthobranchia). Pacific Science 26:381–399.

RUDMAN, W. B. 1999a. *Stylocheilus longicauda* and *Stylocheilus citrina* nomenclatural discussion. Sea Slug Forum: http://www.seaslugforum.net/factsheet.cfm?base=stylnome. Accessed August 3, 1999.

RUDMAN, W. B. 1999b. *Stylocheilus longicauda* (Quoy & Gaimard, 1825). Sea Slug Forum: http://www.seaslugforum.net/factsheet.cfm?base=stylcaud. Accessed August 5, 1999.

RUDMAN, W. B. 1999c. *Gymnodoris striata* (Eliot, 1908). Sea Slug Forum: http://www.seaslugforum.net/factsheet.cfm?base=gymnstri. Accessed September 24, 1999.

RUDMAN, W. B. & P. R. BERGQUIST. 2007. A review of feeding specificity in the sponge-feeding Chromodorididae (Nudibranchia: Mollusca). Molluscan Research 27(2):60–88.

WILLIAMS, E. H. & L. B. WILLIAMS. 1986. The first association of an adult mollusk (Nudibranchia: Doridae) and a fish (Perciformes: Gobiidae). Venus, The Japanese Journal of Malacology 45:210–211.

YOUNG, D. K. 1967. New records of Nudibranchia (Gastropoda: Opisthobranchia: Nudibranchia) from the Central and West-Central Pacific with a description of a new species. The Veliger 10:159–173.

YOUNG, D. K. 1969. The functional morphology of the feeding apparatus of some Indo-West-Pacific dorid nudibranchs. Malacologia 9:421–446.